Integrating digital datasets to quantify morphological variability and understand species delimitation: an innovative approach using terebratulide brachiopods

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What are brachiopods?

- Marine invertebrates
- Lophotrochozoans—related to phoronids, bryozoans, annelids, and nemertreans
- Shells with two valves
- Lophophore—feeding and respiratory organ



Brachiopod diversity through time

- Highly diverse and abundant during Paleozoic
- Dramatic decline after Permian-Triassic extinction
- Current populations seem to be decreasing



Taken from Carlson (2016) adapted from Curry and Brunton (2007)

What drives our research?

- Commonly thought that external morphology offers little resolution for classification in terebratulide brachiopods
- Internal morphology is necessary but rarely analyzed quantitatively
- Testing validity of named species
- Biodiversity estimation



Dallinella occidentalis



Terebratalia transversa



Terebratalia coreanica



Laqueus erythraeus







Laqueus rubellus

Research questions

- Is it possible to discriminate named species based on loop morphology?
- Can we discriminate named species based on shell outlines?
- Is there a correspondence between loop shape and shell outline?



Long loops in brachiopods

- Calcareous structure that supports the lophophore
- Most conspicuous morphological character in terebratulids
- Phylogenetically and taxonomically important



Terebratalia transversa

How do we study long loops?

 To capture the shape and its variability in a quantitative manner, it is necessary to work with 3D reconstructions and 3D geometric morphometrics.



Terebratalia transversa

Methods

| 3D isosurface models | From CT scansAmira | |
|--|--|--|
| Landmark and semilandmark registration | Based on proposed landmark schemesStratovan Checkpoint | |
| Landmark superimposition | Generalized Procrustes Analysis Semilandmark sliding using bending energy | |
| Ordination Methods | Principal Component Analyses (PCA) Canonical Variate Analyses (CVA) | |
| Statistical methods | Procrustes ANOVA | |



R packages geomorph and Morpho

Results—are loops informative?



classification accuracy: 100% Named species statistically different in shape (p=0.001)

Overall





Results—are loops informative?

Laqueus vancouveriensis

- Yes!
- Loops offer sufficient resolution to discriminate between named species.



Laqueus erythraeus

What happens when loops are not present?

- Loops are rarely preserved in fossils
- Are outlines a good proxy for loops?



Terebratalia smithi? Late Pliocene

Laqueus vancouveriensis, Pliocene

Outlines

- Laqueus
- Same specimens as 3D GM analysis
- Outlines of dorsal valve





| Outline digitization | From CT scansIllustrator | |
|-----------------------------------|--|---|
| Elliptical Fourier Analysis | Procrustes Analysis to align outlines EFA | |
| Ordination Methods | Principal Component Analyses (PCA) | R packages Momocs and geomorph |
| Morphological integration | Partial least squares analysisLong loop CT dataset and outlines | |

Outline results



Is there a correspondence between loop shape and shell outline?



Going further

- How can we take these morphological analyses a step further?
- Can we test our morphological predictions using a genetic data?
- Species delimitation analyses using genetic data.

Genetic analysis

Collection of specimens

 East and West Pacific localities • Approx. 10-15 indiv/ loc

DNA extraction and sequencing

- RADSeq—uses restriction enzyme to cut DNA in fragments
- Illumina sequencing

• Single nucleotide polymorphisms (SNPs), heterozygosity, population differentiation

 Maximum Likelihood and Bayesian phylogenetic inference

Species delimitation

Phylogenetic

analysis

• Bayesian analysis of sequence data using the multispecies coalescent model

L. rubellus T. coreanica Terebratalia transversa Dallinella occidentalis Laqueus erythraeus L. vancouveriensis

Pacific Ocean

Conclusions

- We can discriminate named species based on loop morphology. Species are statistically significantly different.
- Shell outlines offer less resolution when trying to discriminate between named species. However, outline data is valuable when loops are not present.
- Importance of treating named species as hypotheses to be tested.
- Importance of accurately estimating biodiversity.

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